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# The Effect of Fluctuating Salinity on the Tissue Water Content of Eight Species of Bivalve Molluscs

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**Summary.** 1. Eight species of bivalve molluscs were exposed both to gradual and abrupt salinity fluctuations and the changes in their tissue water content measured.

2. In 7 of the species studied the tissue water volume varied, but only by a small amount, compared to the amplitude of change of the external medium.

3. Normal *Mercenaria mercenaria* showed no significant changes in tissue water level when exposed either to the gradual or the abrupt salinity regime.

4. *Mytilus edulis* exposed to fluctuating salinity for 1 week prior to sampling showed no significant changes in tissue water content.

5. Wedged-open specimens showed greater changes in tissue water content than did normal animals.

6. The tissue water content of low salinity acclimated *Mya arenaria* increased more quickly in high salinities and decreased more slowly in low salinities than did high salinity acclimated *Mya*. The amplitude of change in tissue water content was greater in low salinity acclimated animals than in high salinity ones.

7. None of the species studied showed an overshoot of the original tissue water content and it seems unlikely that volume regulation by animals exposed to short term salinity fluctuation is due to solute extrusion.

8. A model is presented to characterize each species according to its characteristic permeability.

## Introduction

Bivalve molluscs exposed to fluctuating salinities have been shown to be osmoconformers with some means of mechanical avoidance of osmotic stress (Shumway, 1977). Thus, it is the cells of these animals that must cope with salinity changes of the external medium. Pierce (1971), working with several species of *Modiolus*, raised the question: "Do the cells of these mussels simply swell or shrink passively with the osmotic changes of the extracellular fluids, or does a mechanism exist to regulate the volume of water in the cells?" His studies indicated

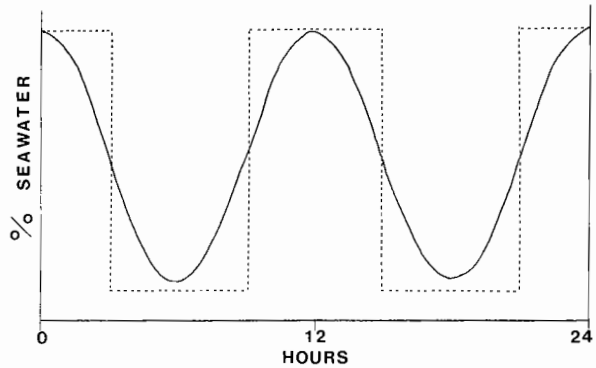


**Fig. 1.** Salinity fluctuation patterns

that the volume of the tissue water varies over the non-lethal salinity range of each species, but only by a very small amount compared to the magnitude of change of the external salinity. Maloeuf (1938) reported that *Mytilus edulis* showed no volume control after 50 hours in dilute salinities. Potts (1958), however, found little difference in the tissue water volume of *M. edulis* adapted to 100% sea water and 50% sea water and suggested that this was due to volume regulation. Two freshwater clams, *Hydriella australis* (Hiscock, 1953) and *Anodonta cygnea* (Florkin, 1938) have been shown to maintain a constant volume in dilute media, but lose weight at higher salinities.

The available data concerning volume regulation in marine bivalves are sparse and often contradictory; and have been derived from steady state experimental conditions. In this study, eight species of bivalve molluscs, representing the sublittoral, littoral and estuarine habitats, were subjected to simulated gradual and abrupt tidal fluctuations of salinity to study the effect of such changes on tissue water content (Fig. 1). To illustrate the importance of shell valve closure both normal and wedged-open animals were used.

## Materials and Methods

Specimens of *Chlamys opercularis* (L..), *Modiolus modiolis* (L.), *Mya arenaria* L., *Scrobicularia plana* (da Costa), *Mytilus edulis* L., *Cardium edule* (L.), *Mercenaria mercenaria* L., and *Crassostrea gigas* (Gmelin) were collected locally from the Anglesey coast. *C. opercularis* and *M. modiolus* were kept at 8 °C in aquaria supplied with running sea water pumped from the Menai Strait (salinity approximately 32‰). *M. arenaria* were acclimated to 20%, 60% and 100% sea water at 15 °C for 4 weeks prior to use. Menai Strait sea water was diluted with distilled water to give the appropriate salinity. All the other species were kept at 15 °C in aquaria supplied with running sea water pumped from the Menai Strait.

The apparatus used to produce fluctuating salinity regimes has been described by Davenport et al. (1975). Shumway (1977) and Hoyeaux et al. (1976) have shown that some species of bivalves are capable of temporarily isolating themselves from the external environment by closing the shell valves. In *Chlamys* and *Mya* such complete isolation is anatomically impossible but the closure phenomenon was investigated by the use of both normal and wedged-open specimens of *M. mercenaria, S. plana, C. edule, M. edulis, C. gigas* and *M. modiolus*. Animals were kept open with small plastic wedges inserted ventrally between the shell valves and cemented to one valve with dental cement. Such wedges allowed the animals to open at will, but prevented them from closing completely. Care was taken to avoid damage to body tissue. All the species were subjected both to gradual (sinusoidal) and abrupt (square-

wave) salinity changes following the patterns shown in Figure 1. Maximum sea water concentration was always 100% (approximately 32‰); minimum sea water concentration varied between programs (see text figures). Experiments with *C. opercularis* and *M. modiolus* were carried out at 8 °C.

Samples were collected for determination of water content from animals in fluctuating regimes every 3 h over a period of 24 h. The animals were prized open and their posterior adductor muscles removed. In the case of *C. opercularis* the entire single adductor was removed. The muscles were blotted dry, weighed, freeze-dried and re-weighed. The total water as a percentage of the wet tissue weight was calculated from the following formula:

$$\frac{\text{wet weight} - \text{dry weight}}{\text{wet weight}} \times 100 = \text{per cent tissue water.}$$

Percentage values for individual animals in a given salinity were averaged and standard deviations computed.

One further experiment in the fluctuating system was performed with *M. edulis*; animals were exposed to a 30% minimum sea water sinusoidal salinity regime for 1 week prior to sampling. Posterior adductor muscles were then removed at 3 hourly intervals and treated in the same manner as other muscle samples for tissue water determination.

For comparative purposes, a steady state salinity experiment on *M. edulis* was conducted. Specimens of *M. edulis* were placed in containers of 20%, 40%, 50%, 60% and 100% sea water. Adductor muscles were collected from animals at each salinity after one week. The tissues were treated as described above.

## Results

### *Mytilus edulis*

Non-acclimated animals subjected to gradual fluctuations of salinity showed significant increases and decreases in tissue water content, but no significant differences were noted between normal and wedged-open animals, as can be seen in Figure 2. In the abrupt regime (Fig. 2), the mussels showed a significant rise in tissue water content during the first exposure to 30% sea water; however, the tissue water content did not return to its original value. There was a significant difference in hydration levels between normal and wedged open animals, the latter being significantly more hydrated.

The mean tissue water content for normal animals both in the gradual and abrupt salinity regimes was $76.4 \pm 6\%$. *Mytilus* exposed to a sinusoidal salinity change for one week prior to sampling showed a constant tissue water level of $75.9 \pm 3\%$ throughout the regimes, as seen in Figure 3. Steady state *M. edulis* exposed to constantly lowered sea water concentrations (Fig. 4) showed increases in tissue hydration, but these increases were not related linearly to the sea water dilutions.

### *Crassostrea gigas*

When placed both in the sinusoidal and abrupt regimes (Fig. 5) *C. gigas* showed significant increases and decreases in hydration level. Unike *Mytilus*, however, there were significant differences between wedged open and normal animals in either regime. Oysters exposed to a 30% sea water minimum abrupt regime (Fig. 5) showed significant fluctuations of tissue water and there were significant differences between normal and wedged-open animals. It should be noted that the differences between closed and open animals were far greater in *C. gigas* than in *M. edulis*.

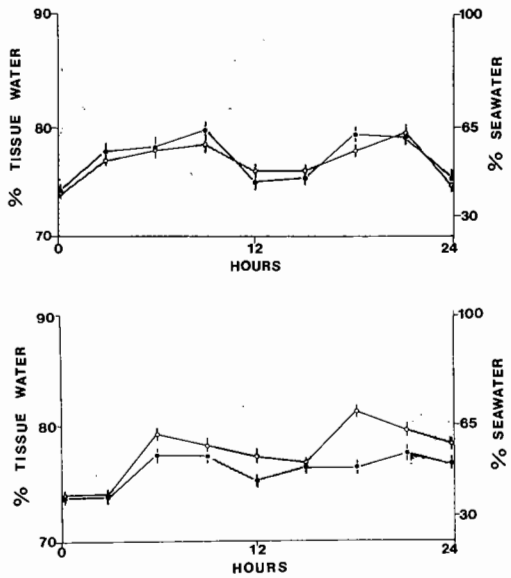


**Fig. 2.** Changes in tissue water content of normal (●) and wedged open (○) *M. edulis* exposed to gradual and abrupt salinity fluctuations. Each point is a mean of 3 animals. Error bars represent 95% confidence limits

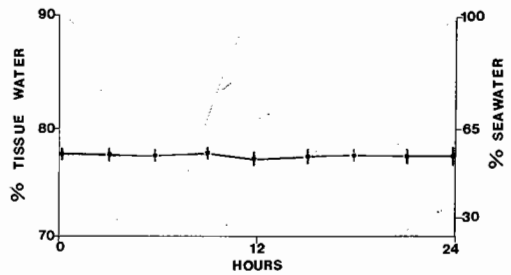


**Fig. 3.** Changes in tissue water content of *M. edulis* exposed to a 30% sea water sinusoidal salinity regime for 1 week prior to sampling. Each point is a mean of 5 animals. Error bars represent 95% confidence limits

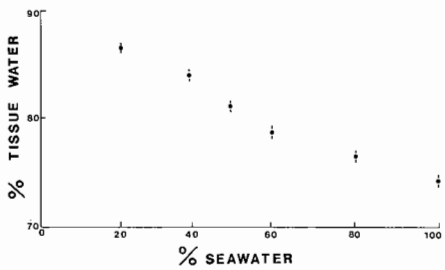


**Fig. 4.** Tissue water content of *M. edulis* exposed to constant lowered salinity for 1 week. Each point is a mean of 10 animals. Error bars represent 95% confidence limits

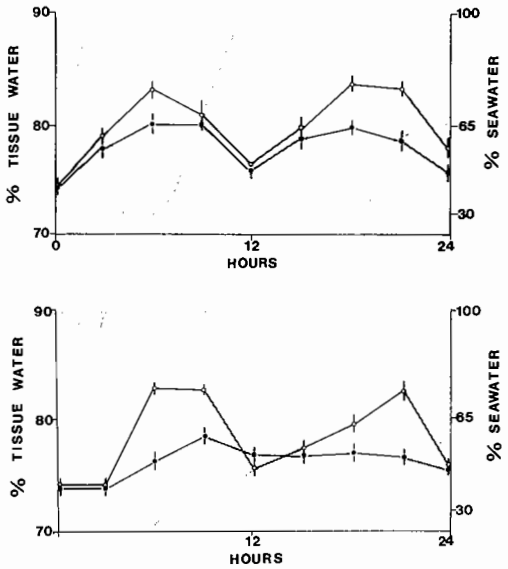


**Fig. 5.** Changes in tissue water content of normal (●) and wedged open (○) *C. gigas* exposed to gradual and abrupt salinity fluctuations. Each point is a mean of 3 animals. Error bars represent 95% confidence limits

*Mya arenaria*

As the mantle cavity cannot be totally isolated from the external environment, only normal animals were used. 100% sea water acclimated clams exposed to a 30% sea water minimum abrupt salinity change (Fig. 6) showed significantly less tissue hydration than those exposed to a 30% minimum sinusoidal regime (Fig. 6).

60% sea water acclimated animals exposed to a 20% minimum sea water sinusoidal regime (Fig. 7) showed a slow rise in hydration as the external salinity decreased and a rapid decrease in hydration when the external salinity increased.

*Mya* acclimated to 20% sea water (Fig. 8) showed an unusual response when subjected to a 20% minimum sea water abrupt regime. The hydration level of the tissues decreased gradually when the salinity rose to 100% sea water, but when returned to 20% sea water, the tissue water content rose rapidly to a higher level than that shown previously in 20% sea water.

*Scrobicularia plana*

In both gradual and abrupt salinity regimes (Fig. 9) *S. plana* shows tissue water fluctuations similar to those of *C. gigas*. There were significant differences in tissue water content between normal and wedged open animals in both abrupt and sinusoidal regimes.

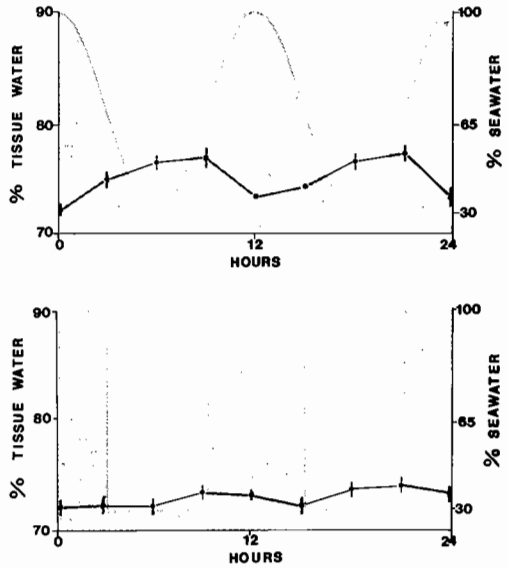


**Fig. 6.** Changes in tissue water content of 100% sea water acclimated *M. arenaria* exposed to gradual and abrupt salinity fluctuations. Each point is a mean of 3 animals. Error bars represent 95% confidence limits

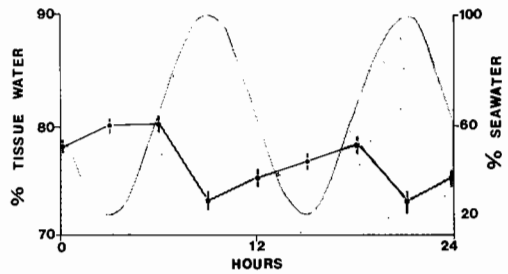


**Fig. 7.** Changes in tissue water content of 60% sea water acclimated *M. arenaria* exposed to a gradual salinity fluctuation. Each point is a mean of 3 animals. Error bars represent 95% confidence limits

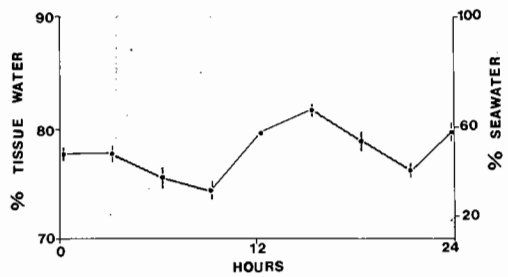


**Fig. 8.** Changes in tissue water content of 20% sea water acclimated *M. arenaria* exposed to an abrupt salinity fluctuation. Each point is a mean of 3 animals. Errors bars represent 95% confidence limits

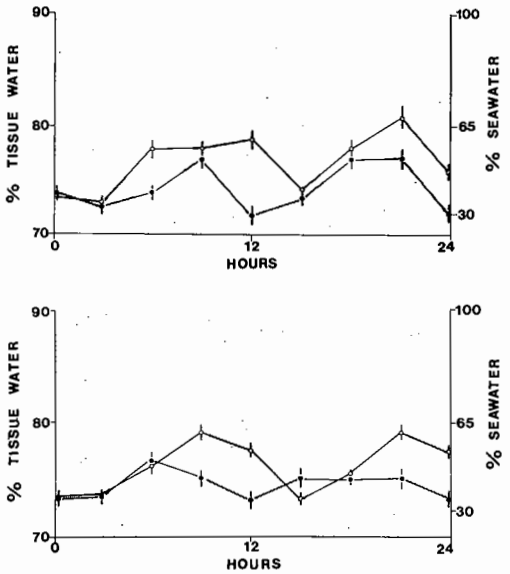


**Fig. 9.** Changes in tissue water content of normal (●) and wedged open (○) *S. plana* exposed to gradual and abrupt salinity fluctuations. Each point is a mean of 3 animals. Error bars represent 95 % confidence limits

*Cardium edule*

Results for cockles exposed both to abrupt and gradual fluctuations of salinity (Fig. 10) are similar to those obtained from *M. edulis*. There were no significant differences in tissue water content between normal and wedged open animals in the sinusoidal regime, but there were significant differences between normal and wedged open animals placed in the abrupt regime.

*Mercenaria mercenaria*

Normal *M. mercenaria* showed no significant changes in tissue water level in the 30 % minimum sea water gradual or abrupt profiles (Fig. 11). Propped open quahogs showed significant fluctuations of tissue water in both the gradual and abrupt regimes.

*Modiolus modiolus*

Normal and wedged open *M. modiolus* showed significant changes in tissue hydration levels both in the 50% sea water minimum gradual and abrupt salinity regimes (Fig. 12). While the hydration levels of propped open animals were significantly higher than the levels in normal animals in both regimes, the difference was most noticeable in animals subjected to abrupt salinity fluctuations.

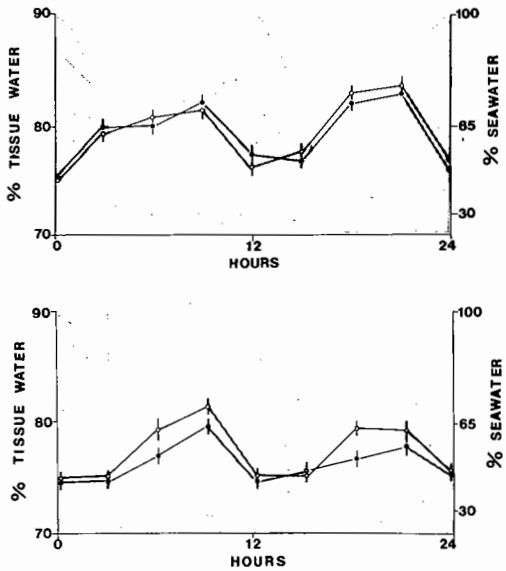


**Fig. 10.** Changes in tissue water content of normal (●) and wedged open (○) *C. edule* exposed to gradual and abrupt salinity fluctuations. Each point is a mean of 3 animals. Error bars represent 95% confidence limits

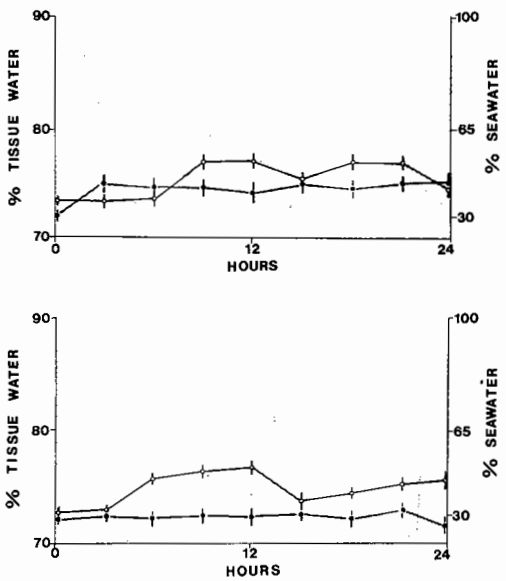


**Fig. 11.** Changes in tissue water content of normal (●) and wedged open (○) *M. mercenaria* exposed to gradual and abrupt salinity fluctuations. Each point is a mean of 3 animals. Error bars represent 95% confidence limits

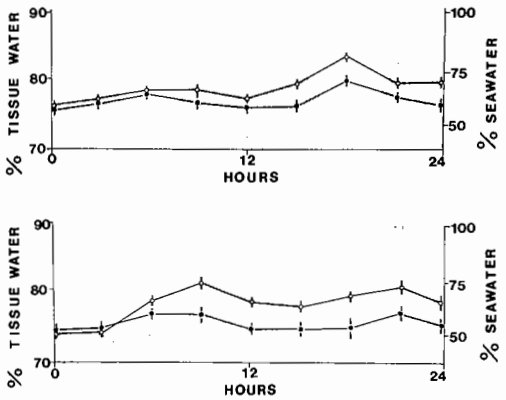


**Fig. 12.** Changes in tissue water content of normal (●) and wedged open (○) *M. modiolus* exposed to gradual and abrupt salinity fluctuations. Each point is a mean of 3 animals. Error bars represent 95% confidence limits

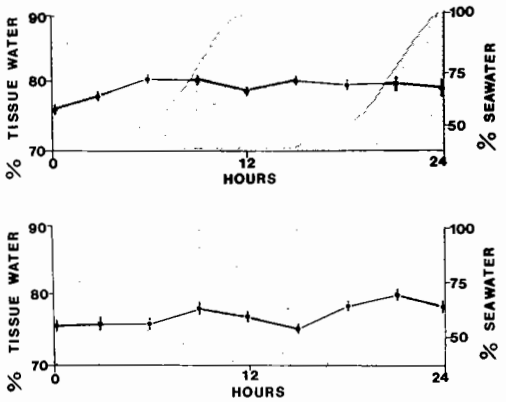


**Fig. 13.** Changes in tissue water content of *C. opercularis* exposed to gradual and abrupt salinity fluctuations. Each point is a mean of 3 animals. Error bars represent 95% confidence limits

### *Chlamys opercularis*

Scallops exposed to 50% minimum sea water gradual and abrupt salinity fluctuations (Fig. 13) showed slight but significant changes in tissue hydration in both regimes. Animals exposed to gradual changes showed consistently higher levels of tissue water than animals exposed to abrupt salinity changes.

## Discussion

None of the species studied showed a return to a hydration level higher than the original 100% sea water control level after a period of exposure to dilute sea water. This would appear to indicate a passive inflow of water to the cells as the external

salinity decreases and likewise, a passive outflow of water during periods of increasing salinity, with little or no solute loss and incomplete volume regulation. In the absence of volume control, an animal exposed to 50% sea water would be expected to double its cellular water content in the absence of any regulating mechanism. The increase in tissue water would be somewhat smaller as the expansion of the cells might reduce the volume of the extracellular fluid. In none of the species tested does the proportion even double. The largest increase is found in *Crassostrea* where, when the water content increased from 75 to 84%, the weight of water associated with 1 g of protein increases from 3 to 5.2, or by 75%. In the other species the increase ranges from 25% in *Mytilus* to 55% in *Scrobicularia*. Even allowing for some reduction in the volume of extracellular fluid, it is clear that the volume of cellular water does not even double. Since none of the species studied showed a significant overshoot of the original tissue water content, it seems unlikely that volume regulation by animals exposed to short term salinity fluctuations is due to solute extrusion.

There are other factors, such as ionic and amino acid regulation, ciliary activity and mucus production that may have an effect on the amount of water that enters the cells. The following model characterizes each individual species according to its permeability ($\lambda$) in a fluctuating salinity regime. The tissue water concentration ($C$) is a direct function of the hemolymph concentration which forms the external environment of the cells ($C_e$).

Hemolymph values are taken from Shumway (1977) and from unpublished data. The following relationship applies:

$$\frac{dC}{dt} = \lambda(C_e - C).$$

The hemolymph concentration of wedged open animals exposed to sinusoidal salinity fluctuations has been found to follow the changes of the external environment (Shumway, 1977) but with a phase lag and reduced amplitude. The external environment, $C_e$ may thus be represented as:

$$C_e = \mathrm{A}\cos\omega t$$

when $\omega$ = angular frequency, A = amplitude external environment (hemolymph).

The characteristic permeability of each species is represented by $\lambda$ and the tissue water concentration is represented by $C$. For the sinusoidal forcing of a non-closing animal we have the following relationship:

$$\frac{dC}{dt} + \lambda C = \lambda \mathrm{A}\cos\omega t = \gamma\cos\omega t, \text{ where } \gamma = \lambda A.$$

Solving this equation for $C$:

$$C = \beta e^{j\omega t} \quad \text{for } C_e = \gamma e^{j\omega t}$$

$$j\omega\beta e^{j\omega t} + \lambda\beta e^{j\omega t} = \gamma e^{j\omega t}$$

$$\beta = \frac{\gamma}{\lambda + j\omega}$$

where $\beta$ = amplitude tissue $H_2O$ change

$$C = \beta e^{j\omega t} = \frac{\gamma}{\lambda + j\omega} e^{j\omega t}$$

$$C = \frac{\gamma(\lambda - j\omega\beta)}{\lambda^2 + \omega^2} (\cos \omega t + j \sin \omega t).$$

Eliminating j, the real parts of the equation are given by:

$$C = \frac{\gamma}{\lambda^2 + \omega^2} (\lambda \cos \omega t + \omega \sin \omega t)$$

$$C = \frac{\gamma}{\lambda^2 + \omega^2} (\sqrt{\lambda^2 + \omega^2}) \cos (\omega t - \phi)$$

where

$$\phi = \tan^{-1} \frac{\omega}{\lambda}.$$

The permeability characteristic, $\lambda$, is given by:

$$\lambda = \frac{\tan \phi}{\omega} = \frac{\tan \left(\frac{2\pi t}{T}\right)}{\omega}$$

where $\omega = \frac{2\pi}{T}$ and T is the period of the input oscillation (fluctuating external environment).

$$|\beta| = \frac{\gamma}{\sqrt{\lambda^2 + \omega^2}} = \frac{\lambda A}{\sqrt{\lambda^2 + \omega^2}}$$

$$\frac{|\beta|}{A} = \frac{1}{\sqrt{1 + \omega^2/\lambda^2}} = \frac{1}{R} \text{ say}$$

$$1 + \omega^2/\lambda^2 = R^2$$

$$\lambda^2 = \omega^2 \left(\frac{1}{R^2 - 1}\right)$$

$$\lambda = \frac{\omega}{\sqrt{R^2 - 1}}.$$

The model results in 2 equations for $\lambda$, one using the period of oscillation (T), the other the relative amplitude ($\beta$/A). For convenience, the latter will be used, although either equation will give the same $\lambda$ value for a given species within the 5 % error margin.

This model applies only to wedged-open animals or animals incapable of shell valve closure depending on the species. When the external sea water concentration falls below a certain concentration, N, the animals capable of closure shut their valves and the following holds true:

$$\text{when } C_e < N, \quad \frac{dC}{dt} = \lambda = 0.$$

Table 1 shows the values of $\lambda$ for the eight species studied in order of descending permeability. It should be kept in mind, however, that these are either wedged-open samples or species incapable of complete closure and therefore, in their natural condition the species' respective permeability may differ from those presented here.

Lange (1964) proposed a three step process for isosmotic intracellular regulation: the osmotic, the intermediate and the regulatory step respectively. During the osmotic step, the primary event is water uptake. The intermediate step is probably composed of the metabolic processes which control final volume regulation. During the regulatory step the regulation of the cell volumes to their normal size occurs and the original properties of the cell membranes are apparently restored. These various periods were easily recognised in the sea urchin *Strongylocentrotus droebachiensis*, but in a subsequent study Lange and Mostad (1967) noted that the events overlap in most animals. The entire process takes 8 days in the sea urchin and in their study of *M. edulis* the animals were adapted to a wide range of sea water salinities for three weeks prior to sampling. Their experiments showed that the muscle cells possessed a pronounced capability for volume regulation, but regulation may not be complete.

Potts (1958) suggested that cellular volume regulation does occur in *M. edulis*. He found that the tissue distension in 50% sea water is much less than the doubling of water content which would occur if the muscles behaved as simple osmometers.

The only other extensive study concerning volume regulation in marine molluscs is that of Pierce (1971). He demonstrated that four species of *Modiolus* (including *M. modiolus*) regulate their cellular volume in dilute sea water by solute extrusion and he concluded that volume regulation in *M. modiolus* is by solute extrusion and appears as a "desperation response" of the bivalve to low salinity water when, after a period of valve closure, the animal is forced to open its valves and make contact with the external environment.

A feature of all previous studies is the fact that the animals were exposed to decreased salinities under steady state conditions for extended lengths of time. For comparative purposes, one steady state experiment was carried out during this study using normal rather than wedged-open animals and the results were similar to those of Pierce, Lange and Potts. It would appear from the data currently available that intracellular volume regulation by solute extrusion, by osmotically conforming animals, is a long term phenomenon and is only attempted as a "last resort".

The data presented here support the "desperation response" theory of Pierce (1971) and indicate that shell valve closure and/or siphon retraction is probably the most important means of volume control in marine bivalves exposure to estuarine conditions. Figures 2, 5, 9, 10, 11 and 12 show the advantage of shell valve closure in

**Table 1.** $\lambda$ values for eight species of bivalve molluscs exposed to fluctuating salinities. Species all listed in order of descending permeability

| Species | $\lambda$ |
|---|---|
| *Crassostrea gigas* | 0.452 |
| *Cardium edule* | 0.431 |
| *Mya arenaria*[a] | 0.429 |
| *Scrobicularia plana* | 0.300 |
| *Mya arenaria*[b] | 0.275 |
| *Modiolus modiolus* | 0.177 |
| *Chlamys opercularis* | 0.177 |
| *Mytilus edulis* | 0.143 |
| *Mercenaria mercenaria* | 0.098 |

[a] 60% sea water acclimated
[b] 100% sea water acclimated

*M. edulis*, *C. gigas*, *S. plana*, *C. edule*, *M. mercenaria* and *M. modiolus*. In general, the differences in tissue hydration levels between normal and wedged-open animals were small or non-existent in sinusoidal salinity regimes; whereas the differences were much more pronounced in animals exposed to abrupt salinity changes, i.e. *Crassostrea*, *Mercenaria*, *Modiolus* and *Scrobicularia*. *Mya*, although not capable of complete shell valve closure is able to retract its siphons, thus isolating itself from the external environment at least temporarily. Those portions of the tissues exposed to the environment are tough and leathery, probably with relatively low permeability to water. In this study, low salinity acclimated animals showed a much higher rate of change in tissue hydration when exposed to fluctuating salinities than did high salinity acclimated animals. This could reflect a high pumping rate in animals exposed to 100% (or rising salinities) and little or no pumping by animals in low salinities. It has been shown (Shumway, 1977) that *Mya* conforms osmotically much faster in waters of high salinity than in waters of low salinity and Matthiessen (1960) found that the rate of feeding of *Mya* decreases with decreasing salinity and that the highest rate of feeding is in water of high salinity, again indicating a decrease in siphon activity and pumping rates in low salinity waters.

Although it is anatomically impossible for *Chlamys* to seal itself completely from the external environment, it can adduct its valves for a short time. This could explain the very slight fluctuations in tissue water when scallops were exposed to gradually changing salinities and the more pronounced tissue water fluctuations in animals exposed to abrupt salinity changes. The period of exposure to lowered salinities is longer in the sinusoidal regimes, but animals in the abrupt regimes are exposed to the *lowest* salinity level for a full 6 h period and it is feasible that the scallops are capable of tonic closure for a long enough period to avoid hydration in the gradual regime, but not in the abrupt regime.

Perhaps the most interesting results were those obtained from *M. edulis* that had been exposed to a sinusoidal salinity regime for one week prior to sampling. After one week, the animals were maintaining a mean tissue water content of 75.9%

throughout the salinity cycle. This value is not significantly different from the mean tissue water content (76.4 %) for normal animals exposed to both gradual and abrupt regimes for a 24 h period. It is suggested that animals exposed to a natural environment of constantly fluctuating salinity do not continually conform to the external salinity, but instead maintain a tissue hydration level that requires the least amount of energy expenditure by the animals. It is possible that after one week, these animals have reached the "regulatory step" proposed by Lange (1964) whereas animals exposed to the fluctuating system for only 24 h never emerge from the "osmotic step".

Another important factor to consider is the size of the animals i.e. tissue surface area to volume ratiol. In dealing with short term fluctuations in salinity large animals will tend to take up and lose less water than small animals, thus giving the impression that large animals are more tolerant. This is not always true, as shown by *Chlamys* (Fig. 14, line B). Although it would appear that there is little water flux (high tolerance) in the scallop when exposed to fluctuating salinities, it is in fact the least tolerant of salinity fluctuations of all the species studied.

It is also true that animals which are very permeable to water will take up and lose more water than less permeable animals, but this factor is also modified by size. Figure 14 shows the regression of hemolymph osmolality upon tissue water content for seven of the species studied. Bearing in mind the short term fluctuating system used, the slopes of these lines essentially reflect dilution rates. Regression formulae are given in Table 2.

The largest animal studied, *Mya* (Fig. 14, line A), shows the smallest water content change for a large change in hemolymph osmolality of the seven species. The smallest animals studied, *Cardium* (Fig. 14, line F) and *Scrobicularia* (Fig. 14, line G) show the greatest water content changes for small changes in hemolymph osmolality. There is no significant difference between lines F and G. There is no significant difference between the lines representing *Crassostrea* (Fig. 14, line C), *Mytilus* (Fig. 14, line D) and *Modiolus* (Fig. 14, line E). It should be noted that these three species are similar in size and lie intermediate between the line representing *Mya* and the lines representing *Scrobicularia* and *Cardium.*

Behavioural responses (i.e. shell valve closure, siphon retraction) to decreasing salinity have no effect on the relationship between hemolymph concentrations and tissue water content; however, they do restrict the concentration level to which the hemolymph will fall.

Figure 15 shows the regression lines for external sea water concentration on tissue water content (Fig. 15, line A) and for hemolymph osmolality on tissue water content (Fig. 15, line B) in *C. opercularis.* The two lines are parallel over the entire non-lethal range, indicating that the scallops are in passive equilibrium with their surroundings and have no means of behavioural control.

Figure 16 shows the regression line for hemolymph osmolality on tissue water (Fig. 16, line B) and the best fit line for external salinity on tissue water content (Fig. 16, line A) in *M. edulis.* Line B indicates that as long as the animals are open and in contact with the external environment the hemolymph is isosmotic with the surrounding sea water and the tissue water content varies accordingly. Line A shows the effects of shell valve closure on the tissue water content. As long as the animals remain open, the two lines are parallel, but when the external salinity

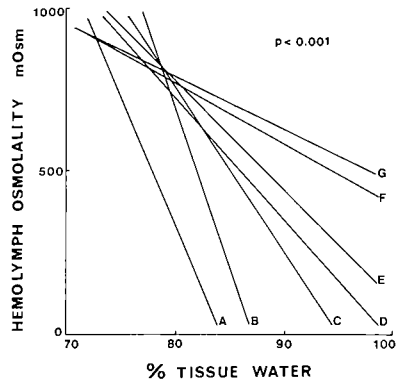


**Fig. 14.** Regression lines for a hemolymph osmolality and tissue water content of *A, Mya, B, Chlamys, C, Crassostrea, D, Mytilus, F, Cardium, G, Scrobicularia* and *E, Modiolus.* Regression formulae are given in Table 2. Osmolality data are taken from Shumway (1977)

**Table 2.** Regression formulae for hemolymph osmolality upon tissue water content

| | | |
|---|---|---|
| *Cardium* | $y = -16.13x + 1984.20$ | $p < 0.001$ |
| *Chlamys* | $y = -84.15x + 7431.32$ | $p < 0.001$ |
| *Crassostrea* | $y = -46.65x + 4468.75$ | $p < 0.001$ |
| *Modiolus* | $y = -32.40x + 3376.07$ | $p < 0.001$ |
| *Mya* | $y = -72.38x + 6183.13$ | $p < 0.001$ |
| *Mytilus* | $y = -40.39x + 3968.58$ | $p < 0.001$ |
| *Scrobicularia* | $y = -15.08x + 2000.46$ | $p < 0.001$ |

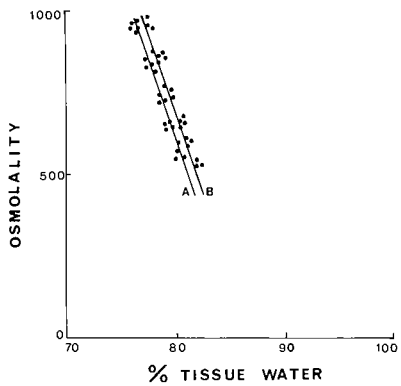


**Fig. 15.** Regression lines for external sea water concentration on tissue water content (*A*) and for hemolymph osmolality on tissue water content (*B*) in *C. opercularis.* Osmolality data are taken from Shumway (1977)

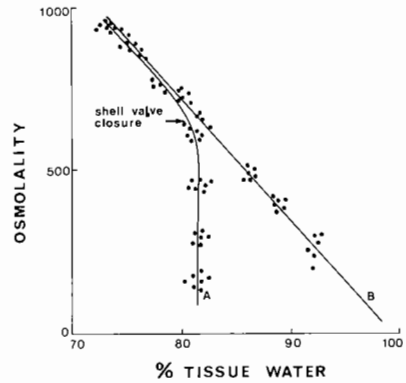


**Fig. 16.** Regression line for hemolymph osmolality on tissue water content (*B*) and the best fit line for external salinity on tissue water content (*A*) in *M. edulis*. Osmolality data are taken from Shumway (1977)

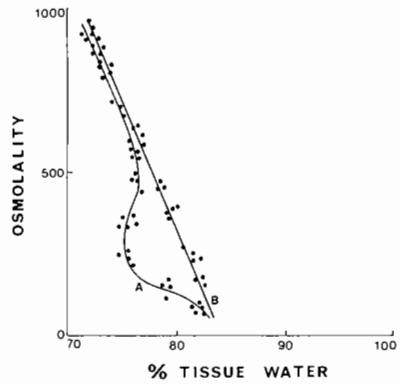


**Fig. 17.** Regression line for hemolymph osmolality on tissue water content (*B*) and the best fit curve for external salinity on tissue water content (*A*) in *Mya*. Osmolality data are taken from Shumway (1977)

reaches ~500 mOsm (Shumway, 1977) the animals close their shell valves and hemolymph dilution ceases. This in turn causes the tissue water level to remain constant, yet does not alter the relationship between hemolymph osmolality and tissue water content.

The regression line for hemolymph osmolality on tissue water (line B) and the best fit curve for external salinity on tissue water content (line A) for *M. arenaria* are given in Figure 17. Line B, Figure 17 shows that as the hemolymph osmolality decreases, the tissue water level increases. *Mya* shows the typical response of a reasonably efficient estuarine osmoconformer in that in very low salinities the high level of tissue hydration is partially reversed. In high salinities, the animals are in passive equilibrium with the external medium. It should also be noted that the overall permeability of high salinity acclimated *Mya* was found to be less than low salinity acclimated animals.

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